Topological coding in hippocampus

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The proposed analysis of the currently available experimental results concerning the neural cell activity in the brain area known as hippocampus suggests a particular mechanism of spatial information and memory processing. Below it is argued that the spatial information available through the analysis of the hippocampal cell activity is predominantly of topological nature. It is pointed out that a direct topological analysis can produce a topological invariant based classification of the cell activity patterns and a complete topological description of animal's current environment. It also provides a full first order logical system for local topological reasoning about spatial structure and animal's navigational strategies.

I.   INTRODUCTION

The task of space perception and spatial orientation is one of the most fundamental tasks faced by animals. The animal perceives itself and the surrounding environment, plans and executes its movements and its behavior in the context of the space that it experiences through neural activity in its brain. Currently, there exists significant experimental data concerning the mechanisms of spatial encoding based on electrophysiological recordings from human, primate and rodent (notably rat's) brain. These experiments suggest a number of specific principles according to which computation about space in the brain is organized. Below we review some of this physiological and experimental data regarding the structure of neural space processing with the aim of introducing a certain view on the principles of space discernment in biological neural networks. This approach emphasizes that the phenomenon

of space perception does not reduce to a passive reflection of the spatial organization of the external stimuli, but primarily is based on an active construction of the brain's own internal spatial framework.

The paper is organized as follows. Section II describes some basic experimental facts about neurophysiology of space coding and outlines some of the current paradigms used for analyzing neural activity patterns. A short supplemental list of physiological properties of the hippocampal neural cells is given in the Appendix. Section III discusses space description and space perception tasks in general terms, and outlines a specific structure of spatial information analysis that will be used in the rest of the paper. In Section IV we formulate a specific spatial information analysis task that motivates a particular approach to studying hippocampal space coding activity. It allows us to propose a hypothesis about the topological nature of the hippocampal space coding mechanism, which is further discussed in Section V in light of data obtained in continuously deforming environments. A discussion of the experimentally studied bounds of the continuous change regime is given in Section VI.

An analysis of the PC population responses in Section VII is provided to support the claim that activity of these cells is globally coherent and may produce the emergent phenomenon of a physiological spatial frame (the "inner space") that serves as the basis of animal's spatial awareness. The topological properties of this space are analyzed in Section VIII, where it is shown that its invariant characteristics match the characteristics of the observed experimental environment. Section IX introduces the idea of using qualitative space representation analysis of the spatial information, in particular the Region Connection Calculus that allows the logic of animal's spatial behavior both in static and in slowly changing environments to be followed. A short discussion in Section X puts this study into perspective of other theoretical analyses of neural space coding mechanisms.

II. GENERAL PROPERTIES OF THE PFS

In electrophysiological experiments, functional properties of the neurons and the neural networks are identified by studying statistical correlations between neural activity patterns in wake animals and various external (sensory) and behavioral parameters. One such functional property of neurons was found in 1971, when O'Keefe and Dostrovsky discovered that the firing activity of the pyramidal cells in a rat's hippocampus has clear spatial correlates
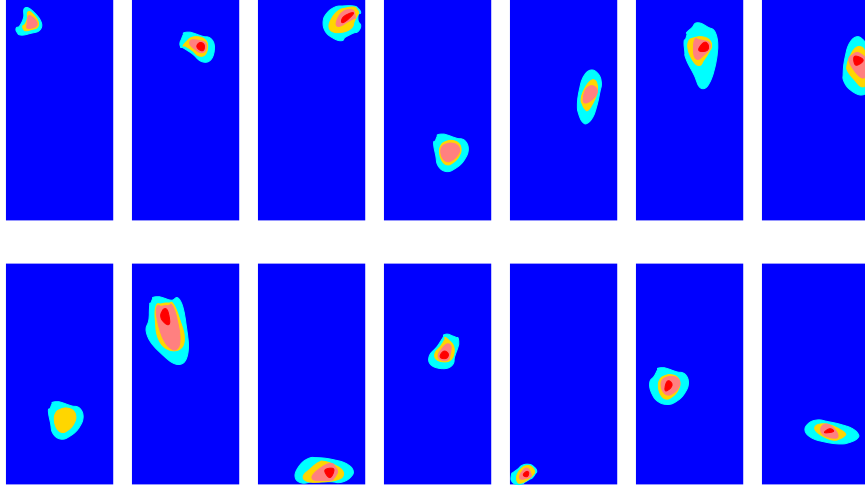
FIG. 1: A schematic representation of the place fields of 14 place cells in a square environment. Color code represents the increase of the firing rate from the background (blue) to highest level (red).

[147]. Specifically, it turned out that these cells become active only in a relatively small portion of the environment and remain basically silent elsewhere (Fig.1). Hence these cells (called "place cells", PC) highlight a certain system of regions (called "place fields", PF), i.e. define a system of spatial "tags" via their firing activity. The exact organizational and computational principles that produce place specific firing patters or different PF partitions of the environment are still not known, however there exists a general consensus about the overall purpose of the PCs. It is thought that the PCs discretize continuous flow of the sensory input into an inhomogeneous map, by using qualitative features of the environment. The behavioral and functional significance of the hippocampus has been demonstrated in variety of experiments. It has been shown that if the hippocampus is partially or completely damaged, impaired or knocked out, the animal looses its full ability to solve many spatial navigation tasks, especially tasks based on following sequences of cues and retrieving sequential (episodic) memories [64, 107, 108, 177]. Experimental evidence indicates that the collection of the PFs completely covers the whole environment that is recognized by the animal as "familiar", and that the PFs reflect the structure of rat's internal map of this environment. It is believed [64, 177] that this map serves as one of the key structures of rat's
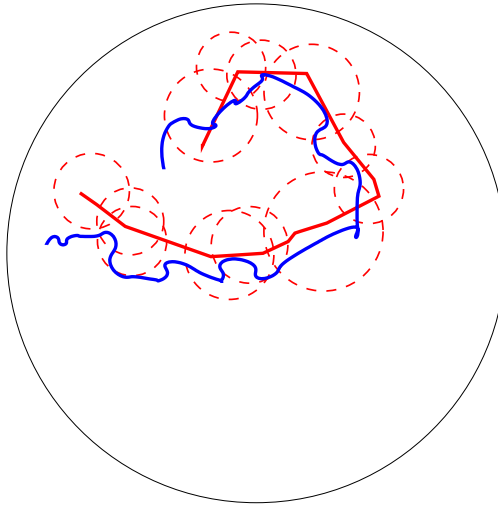
FIG. 2: Schematic representation of the trajectory reconstruction based on the place field activity [74]. Blue line represents the actual trajectory or the rat, red circles show the recorded place fields, the red line represents the reconstructed trajectory. The accuracy of specifying rat's current position depends on the number of PFs with known locations in the arena and their sizes.

spatial awareness, which was therefore named "cognitive map" by O'Keefe and Dostrovsky [148].

It was also shown in [27, 204] that knowing the positions of a relatively few (70-80) PFs in a small (about 1 m across) environment, one can predict the rat's location at any time with an impressive accuracy (Figure 2) based on the current pattern of the activity of its PCs. A simple extrapolation of the results of this experiment suggests that an external observer should also be able not only to reconstruct the rat's current location and trajectories as in [27, 119, 204], but also to characterize the whole space as it is encoded by the hippocampus, based on the information contained in the PC activity configuration. We hypothesize that the analysis of the PC activity should provide an insight into the organization of the inner or "physiological" (in the terminology of [148]) space that emerges from the spiking activity of the neurons.

Usually, the analysis and the interpretation of PC firing patterns is based on correlating the firing events with the features (e.g. geometric) of the physical location where firings have occurred. Thus, the properties of PFs are usually defined in terms of the sizes and the shapes

of areas where the corresponding PCs are active. This perspective assumes an external observer. From the point of view of the regions receiving PC input, proper description of the spatial representation of the environment should not depend on the external characterization of the firing patterns and rely only on the intrinsic information encoded in the temporal structure of neural activity. From such a perspective, understanding the mechanism of space perception depends primarily on the possibility of interpreting the spiking activity from the "proper" point of view of the system, i.e. understanding the meaning of the computation in the hippocampal network as it translates the *temporal* pattern of the firing activity into a *spatial* pattern of the firing fields.

III. INNER SPACE AND THE SPATIAL PERCEPTION TASK

In this discussion, the term "inner space" is used to emphasize the point that the spatial representation in the brain does not reduce to a passive reflection of the sensory input. Rather, the state and the activity of the brain bring about a separate *emergent* phenomenon of an inner space, that is an object in its own right. It is this emergent physiological inner space, rather than an "objective physical external space" that is directly experienced and perceived by the animal, in which the animal actually plans and executes its behavior, navigational tasks, etc.

There is a profound difference between the neural activity merely *reflecting* the external input by producing reliable responses, and an activity pattern that *amounts* to having a separate internal representation of a space, defined in a certain specific mathematical sense. Clearly, the full task of space representation requires a variety of different computations that integrate sensory information into several complementary space representations. The analysis of the hippocampal PC activity outlined below suggests that the PF map may provide the most basic, topological level of the inner space coding.

The precise mechanism of space coding and even the scope of computational tasks that the animal must address in order to achieve a sufficiently complete space representation is unknown. However, from the mathematical point of view, the colloquial term "space" implies a complex assembly of several conceptually different structures, that must be coherently brought together to produce the familiar realm of "space". These structures include:

1. Topological order, i.e. the relationships of adjacency and spatial connectivity, spatial

interior, boundary, closure, which allow the most general and a highly abstract representation of the notion of spatial continuity. Topological properties are preserved through deformations, twisting and stretching of the space. They express whether the space can be separated into parts, or contains "holes", etc., and are not sufficient to express "sizes" or "shapes".

2. Affine structure – the possibility to define directions (vectors) at a given point and a possibility to relate directions at different points in a way consistent with the adjacency relationships and scale at different locations in space. The ability to measure arcs, i.e. the angles between two directions. The possibility to combine consistently the angular and the distance measure. This is necessary to define geometrical objects, e.g. straight lines, circles, and in general – forms, contours, rigid bodies, and the relationships between them.

3. Metric information – a quantitative description of various spatial scales via a topologically consistent distance measure between objects. This construct allows the introductions notions of "more close" or "less close", rather than just purely topological "adjacent or not". Establishing a global metric amounts to imposing a globally consistent system of scales at different points, i.e. the general notion of size.

It is not clear a priori that this or similar stratification of the spatial coding task is implemented in the brain. However, it will be argued below that the task of encoding a topological representation of the spatial order is addressed by the hippocampal PCs, whereas other brain systems provide metric and affine information in order to provide the animal with a complete spatial representation of the environment. The latter include the cells that signal the instantaneous head direction of the animal regardless of the location of the animal in the environment [138, 159, 183, 184]. The information about an animal's orientation, direction and duration of its travel is also represented in the *ego*centric spatial frames encoded in the parietal cortex [8, 9, 10, 31]. Metric information is likely provided by proprioceptive (feedback from muscles and joints) and idiothetic (self motion) cues [187], based on visual, vestibular [133] sensory inputs. In contrast, the hippocampus, which is functionally the highest associative level network in the brain [12, 112], encodes and supplies the most abstract representation of the space – the allocentric topological map, that serves as a "locus" [29] of an animal's spatial awareness.

Importantly, there exist certain mathematical frameworks that allow the question in what sense firing of the neurons in various parts of the brain may *amount* to the space that the animal perceives to be addressed. In the familiar approach, commonly used in mathematics and mathematical applications [5, 25, 106], the space is understood as a certain proximity, scale and affine structure defined on a set of elementary "locations" – the points of the space. In such an approach, the topological spatial structure emerges as a matter of associating subsets of points (originally unrelated spatially) into a consistent system $\mathfrak{U}$ of "neighborhoods". The consistency conditions (Kuratowski-Hausdorff axioms [5]) require that arbitrary unions and finite intersections of the subsets from $\mathfrak{U}$ never produce subsets that lie outside of $\mathfrak{U}$. This guarantees that the chosen subsets can actually be considered as "proximity neighborhoods" in the conventional geometrical sense and that they generate a topological space structure on the original set of points.

Interestingly, the proximity structure does not have to be applied to a set of infinitesimal elementary locations. Instead, the neighborhoods *themselves* can be understood the primary objects, so the proximity relationships are imposed on *regions*, rather than points. In such approaches (unified under the name "pointless topology" [58, 101, 143, 199, 201], or alternatively by the term "mereotopology" [48]) points are secondary abstractions, produced by intersections of a sufficient number of regions. The analysis of the topological connections between the regions in point-free spaces reveals a particular structure of logical and algebraic relationships between them that define the spatial organization. As a result, the pointfree topological space emerges from a logical/algebraic ("*locale*" [101, 196]) structure imposed on the infinite set of regions [101, 102, 103, 111, 136, 165, 196, 201].

It is clear however, that the quasitopological inner space generated through the activity of a finite number of the PCs in the hippocampal network can be defined in terms of only a finite set of regions or spatial relationships. In this sense, the inner space appears as a qualitative, finite approximation to the idealized continuum space. Physiologically, both the set of spatial regions and the continuity relation are derived through some discretized representation of the sensory input, and then used to internalize the external sensory structure in the form of a relatively coarse, qualitative space. In particular, the quasitopological aspect of the animal's inner space seems to be founded in certain qualitative region-based spatiotemporal reasoning schemes that provide discrete, qualitative versions of the standard set-theoretic or abstract "pointless" space computations.

Overall, the task of representing the space through neural activity can be considered as an interesting and practical (also empirical) case of mathematical constructivism, in which one aims to describe the emergence of a topological space based on the firing mechanisms of neural cells. The pointfree, region based space construction approach seems to apply directly to the task of space coding in biological networks, which compute e.g. the hippocampal quasitopological frame of the inner space from finite regions – PFs.

IV. PLACE FIELD PARTITIONS

As described in the previous section, the geometrical information contain in the observed system of PF can be used to reconstruct an animal's navigation paths and potentially describe certain aspects of the space as a whole based on the current PC activity. It is important however, that the information contained in the PF partitions alone is insufficient to represent the full extent of spatial relationships that are used and perceived by the animal. Some examples of spatial relationships that are *not* encoded via a "place tag" system are e.g. the observed sizes of the PFs themselves, the distances or the angles between PFs or between the external cues. In order to obtain such characteristics, the PC information must in general be complemented by additional information, e.g. rat's speed, the direction and the duration of straight runs and turns, etc.. In order to address the nature of the spatial information encoded in the PFs, it will convenient in the following discussion to refer to the following

- **Space reconstructing thought experiment (SRE)**: Imagine a rat that is running on a certain arena, separated from the experimenter (the observer) in a locked room. The experimenter receives the real time signals from the electrodes that are implanted into the rat's hippocampus, and is free to analyze the recorded information in any way in order to extract from it as much information as possible about the geometry of the arena and about the navigational task faced by the rat.

  Question: how much would the experimenter be able to deduce about the geometrical and spatial properties of the environment based on the PC activity?

Comment: The firing patterns of the PC can in principle contain more information than provided by the spiking probabilities alone. Additional navigational and spatial information,

such as the size and the shape of the PFs, etc., can potentially be supplied through other parameters, such as the structure of the spike trains of single or multiple PCs, temporal structure of the cell bursting, or additional PF ensemble correlates. However, currently there is no evidence that there exist correlations between such parameters and the angle or the scale coding. With these stipulations, we will disregard below such "fine structure" coding of the spike trains.

With this understanding of the PF functionality, let us start by considering the SRE task in the simple case of a rat running on a linear ($1D$) track. After observing the PC signals for a sufficiently long time, the observer in the thought experiment described above will notice that there is a linear order to the time intervals in which hippocampal cells are active. Assuming that the experimenter knows that the firings are spatially correlated (i.e. that he in fact deals with the PCs), this would lead to the conclusion that the environment is linear. In more complex ($2D$ or $3D$) environments the correspondence to the spatial order is less direct, however a careful analysis of the firing activity of a sufficient number of cells (for more formal discussion see Sections IX and VIII) should suggest to the observer that the temporal pattern of spikes is consistent with a possible ordering of regions in a space, i.e. that the firing events can serve as a consistent system of spatial location labels.

It is important to notice however, that given PF variability, this system of spatial location tags a priori provides the observer only with *spatial order* relationships and does not contain in itself any information about the scale, the size or the shape of the environment. For example, in the case of a SRE analysis of a $1D$ track it will be impossible to say, through a mere observation of the PC activation sequences based on the properties of the PFs listed above, whether the track is straight or bent (i.e. whether it is I-shaped or U-shaped or C-shaped or S-shaped or J-shaped), what is the scale of the environment, i.e. how long is the track or what is the curvature scale of its sections. In order to produce a more complete spatial description, the information about the sequence of locations should be associated with the scale and the angle information. As mentioned above, such information can be deduced from supplementing the time courses of the PF firing with the information about the speed, direction and duration of motion, etc., all of which do not correlate directly with the PF locations. Based on the PC average activity profile alone, one can only determine whether the track loops (O-shaped) or how many open ends it has (i.e. whether it is X-shaped or J-shaped, however J-shaped and U-shaped tracks are indistinguishable).

In the absence of any evidence of direct geometrical information contained in PC temporal coding, we arrive at the hypothesis that the hippocampal place cells encode predominantly the *topological arrangement of the spatial locations* – the topology of the inner "physiological" space.

It should also be mentioned, that although many of the shapes discussed above (e.g. W and I) are topologically identical, at the level of structural (e.g. sequential) organization of the available spatial locations, it is possible to separate each shape into connected parts, and to describe the topology of the assembly. The fact that the sum of some pairs of parts can be shrunk to a point but others cannot is the distinguishing feature, discussed in more detail in Section IX. As mentioned above (item 10 of the PF properties list in the Appendix), truck junctions and other distinguishing features in the space are typically explicitly coded for by the CA1 place cells [30, 150]. In the context of the topological space coding, these features effectively play the role of spatial singularities and "marked points" that limit the "topological plasticity" of the space.

In view of this hypothesis, it is also significant that the hippocampus is known to be largely responsible for "sequence coding" on a variety of different time scales, even on the cognitive/behavioral level. Experimental evidence indicates [2, 26, 41, 56, 63, 69, 99, 107, 108, 132, 179, 198] that the behavioral performance of the animals with hippocampal lesions in goal-directed sequence tasks is significantly reduced compared to the control animals. Hence it appears that the hippocampus supplies current representation of the consistent discrete sequential structure of the environmental features, navigational cues and behaviorally relevant memories.

In a spatial context, such a regime of memory processing is in effect synonymous to representing topology. It is well known that the topological structure of a space can be defined not only descriptively, via a set of topological invariants [146], but also constructively, via an explicit, detailed set of discrete connectivity relationships between regions of the space [48, 58, 101, 102, 103, 111, 136, 143, 160, 165, 196, 199, 201]), which appears to be the basis of the hippocampal coding mechanism.

V. STABILITY WITH RESPECT TO GRADUAL CHANGES

Interesting evidence in support for the topological coding hypothesis comes from the analysis of the PF responses to the alterations of the environment. Remarkably, if the external parameters, the "features of the environment" are changing sufficiently slowly, gradually, then neither the number of PFs nor their relative order change, only the exact location of PFs and the shapes of PC's activity distribution profiles, i.e. the firing frequencies. So there exists a certain regime of continuity in the representation following sufficiently smooth changes in the external world. A number of studies have demonstrated that gradual changes of local and distal cues in the familiar environment produce a variety of orderly responses from the PFs, while maintaining their *relative* positions with respect to external cues and each other. For example, a sufficiently slow dimming of lights, or gradual addition of odors, or a smooth changes of the floor texture or a combination of such changes does not produce changes in the mutual order of the PFs. If a rat is taken from one square arena to another, similar enough for the rat to recognize the similarity, then the PF mapping of the new environment remains the same [115]. In other words the operating regime of the network, its synaptic strength configuration $S^{(i)}$, observed via PF layouts, does not undergo a major restructuring in order to track these changes.

It should be noticed however, that due to the fact that the environment transformations in a typical experiment involve many parameters that may affect miscellaneous aspects of hippocampal and cortical information processing, different functional responses in such experiments are often mixed together, which obscures regularities in PF behavior. For example, it was shown that moving separate objects in the arena, or creating a particular sensory cue dissociation [67, 139], as well as a special animal training protocol [116] may lead to a variety of responses that sometimes violate the original spatial pattern or the firing regime of the PF (e.g. rate remapping, [95, 116, 117]). However precisely because of the structural and functional heterogeneity of the external input, these variations usually do not directly support or oppose the topological coding hypothesis.

Since the hippocampus is known to be involved into complex memory formation and consolidation processes in interaction with other brain parts, e.g. the neocortex, it is clear that the implementation of each hippocampal PF map may reflect various information about the environment, the objects within it as well as arbitrarily complex relationships between
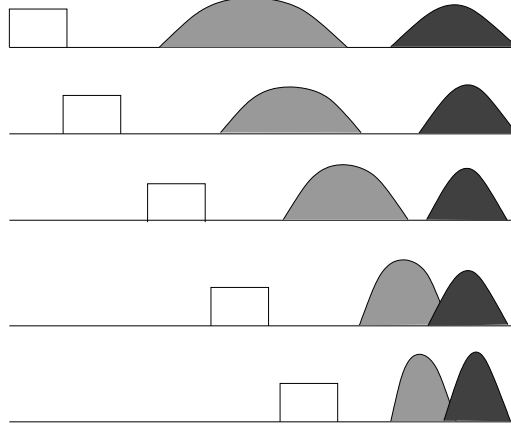
FIG. 3: Schematic representation of the elastic stretch of the PF layout reported in [85].

them. Therefore, in the context of studying specifically spatial aspects of hippocampal activity, it is important to specify a particular type of external transformation that can adequately address and bring forward specifically spatial aspect of the PC responses. For that purpose it is natural to consider spatially consistent, *geometric* changes, in which the whole set of sensory stimuli changes coherently, so that the mutual spatial order between every set of sensory cues is preserved and to study the of the PCs to this specific type of transformations. This approach is crucial for interpreting e.g. the phenomena of the partial (rate) remapping [117] that appear as a result of separate cue manipulations.

The organized response of the PFs to the geometrical changes of the environment was revealed in a particularly interesting group of experiments, [67, 84, 85, 139, 149]. In these experiments the shape of the environment is gradually altered (via a discrete sequence of transformations), and the positions of the PFs from the same PCs are recorded before and after the transformation. The results show that if the changes are sufficiently smooth, the positions of the PFs follow continuously the change of the geometry of the environment, i.e. they drift continuously in the physical space without changing the original relative activity structure.

More importantly, this connection is not local – the responses of the place fields to the geometry alterations may be highly correlated across the whole environment. According to experiments of Gothard et. al [84, 85, 86] the overall pattern of the PFs on a linear track shifts elastically in response to stretches or compressions due to the move of one of the track's ends (Fig. 3). Not only the PFs located next to the moving end respond by

shifting, but also the rest of them, all along the track, shift accordingly to their distance to the moving end. The overall response pattern of PFs is as if they were drawn on an elastic sheet that can stretch or compress with the shifts of parts of the environment.

A particularly important aspect of these results is that the PFs are not in fact anchored to a specific area of the environment. Instead, a particular stable configuration of the hippocampal network seems to enforce only the *relative* pattern of the PFs. The resulting global discrete map is in effect superimposed, projected onto the environment and that is preserved in continuous geometric transformations of the external cues. It is this hippocampal network configuration, and the corresponding structural pattern (a specific implementation of the cognitive map) that is directly available to the animal and may form a quasi-topological internal basis of an animal's spatial awareness.

This illustrates one of the core points of the proposed approach, namely that in a stable configuration of the hippocampal network, the activity pattern of the ensemble of the PFs codes for the relative order, rather than the for association between the regime of elevated activity of a particular cell and a specific external location, object or an event.

Such a view allows to comment immediately on the property of allocentricity of the PFs, i.e. the independence of the PF locations on an animal's body position, behavior, etc. (see item (7) in the Appendix). Indeed, if for a given cell, the location of its PF primarily reflects the *order* in which it fires with respect to the other cells in the network, the association between the regime of its elevated activity and a particular external region (its firing field) is a part of the global association of the whole hippocampal configuration with the structure of the environment. Clearly, if the relative activity regimes of PCs in a given network configuration are fixed, the externally observed PF pattern does not change as long as the network configuration remains the same. If an animal's behavior, its orientation and other similar characteristics do not affect the order relationships coded in the hippocampus, the activity of each cell is projected onto the same corresponding region, so the projected location of the PF on the environment will be allocentric. In "morphing" environments, if the same configuration is projected onto a deformed arena, it creates the effect of the "moving" PF for an external observer.

If the geometric (or in some cases non-geometric [139, 140, 141]) transformation is a superposition of several dilations or homothetic transformations, there appear to be different groups of cells that follow a particular component of the deformation, thus forming a par-
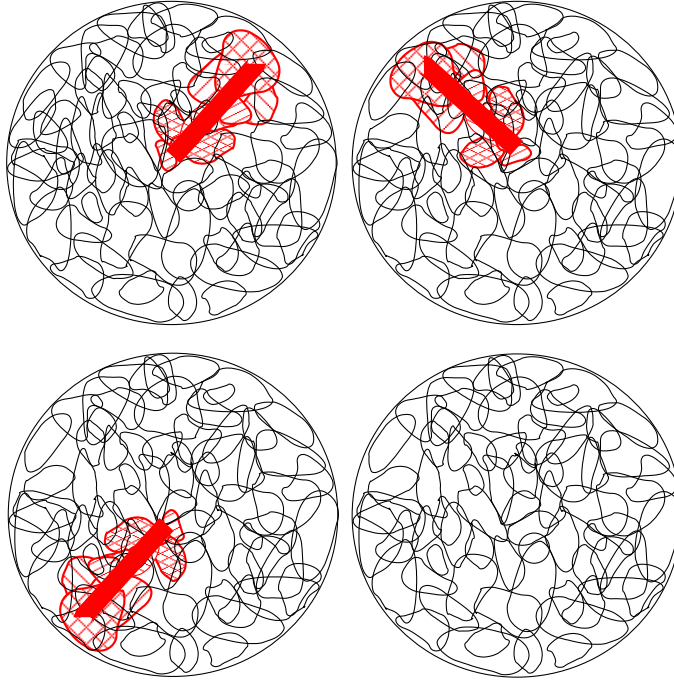
FIG. 4: Schematic representation of reference frames of place fields in a circular arena with a moving barrier (red bar). Red shaded regions represent the barrier bound PFs that move with the barrier.

ticular "reference frame" [85]. In the experiment [85] in which the walls of the environment were rotating while the floor and some objects scattered on it were static (or vice versa [139, 140]), one finds a subgroup of cells whose PFs were bound to the walls (wall frame) and another subgroup of PFs that remain floor [85] or object [139, 140] bound. For example, the PFs that are located close to the shifting wall segments or moving barriers seem to be moving with them, so PFs are actually tied to the elements of the environment. This indicates that the space representation is layered in a certain way.

Hence, based on the existing experimental evidence it seems reasonable to conjecture that in general the number of the frames is given by the number of the geometric components of the transformation and of spatial/behavioral modes. The latter possibility has been recently reported in [113], where it was observed that the closed linear structure of the environment produced a separate frame – a subpopulation of PFs that drift continuously along the closed

path on a quasi-linear track without violating mutual order. The following discussion will focus either on geometrically simple transformations or on one such layer or a reference frame.

For the case of a single geometric transformation as in [85], it is clear that since in the course of such changes the mutual order of the PFs does not change, the spatial information that the PFs encode (from the point of view of the SRE observer) remains the same. Therefore, although the times at which neurons produced spikes may change, the SRE observer (the hippocampal homunculus) can not follow the deformation of the environment through this change. Hence, since the *structural pattern* of the activity is preserved, i.e. the hippocampal network is encoding the same set of the relationships through sufficiently gradual geometric transformations and thus represents the same spatial information throughout the change. In other words, this type of the receptive field plasticity associated with the invariance of the mutual order of the receptive fields suggests that the space representation by the hippocampal network is invariant with respect to sufficiently smooth geometrical distortions of the environment, and hence provides a certain *flexible* (for the external observer) discretized representation of the behaviorally relevant spatial information. So in that sense the PF patterns encode the "elastic skeleton" of the space represented in rat's brain, i.e. provide the information of topological nature.

We further hypothesize that results similar to Gothard et. al. will be found for more general alterations: if the environment changes its geometric configuration (stretches or bends) sufficiently slowly, then the PFs will follow this change in the sense of [85, 86], so the temporal *order* of the firing sequences will remain invariant.

The above arguments require certain additional stipulations about neglecting the "scale" effects that may arise due to the finite size and the firing profile of the PCs. For example, PFs have a certain range of characteristic sizes, which imposes a restriction on the scale of the changes that may be ignored by the hippocampal network: the scale of changes per cell should be less than or comparable to the characteristic size of the individual place field. Also, the excitation level of a PC increases as the rat is getting closer to the center of its PF, which may provide some *local* metric and directional information, within the scale of (a priori unknown) size of the PF, which does not change the argument about the topological nature of the space coding in PF population.

Overall, these results suggest that PFs code for the topological information in the con-

ventional mathematical sense in at least in two aspects – as a consistent collection of places that expresses spatial order, which (as a matter of empirical coincidence) has the "elastic grid" properties, i.e. is invariant to a certain range of geometrical transformations. Below the spatial discretization mapping will be referred to as *quasitopological*, to emphasize that the topological regime is stable only within a certain range of parameters, which limits the scale and the time course of the external changes.

VI. REMAPPINGS

Experimental evidence also suggests that significant and/or rapid changes may cause a complete change of the representation – the so-called remappings, in which the old pattern of PFs is replaced by an entirely new one. In the remapping process cells may completely change their firing properties: some previously quiet cells may become active, previously active cells may shut off, and the overall PF location pattern acquires a completely different structure. For example, in the experiments with a thin barrier placed into the arena (Fig.5), the PFs on which this barrier was placed disappeared, i.e. the corresponding PCs stopped firing there, although the rat could physically visit most of the place occupied by the disappeared PF from both sides of the barrier. If large (compared to the size of the arena) barriers are added or removed, so that the geometry of the environment, e.g. the available navigational routes, change significantly (Fig. 5), then the PFs pattern can remap not only in the vicinity of the barrier, but also in the rest of the arena [78, 174, 175, 177]. During such remapping processes, the strengths of the synapses may reset [141] and so the hippocampal network transitions into a different state $S^{(j)}$. Experimental evidence also indicates that abrupt geometric deformation can also cause remappings; however the slower are the changes the larger is range of changes that do not cause a major remapping.

The organized response to the external changes, in which the quasi-topological order of the PFs is preserved and the abrupt scrambling of the PF order represent two qualitatively different regimes of behavior and of spatial coding. A simple example of remapping is provided by the violation of the linear order of PFs on a $1D$ track following the abrupt changes of the track configuration. The remapping here corresponds to a violation of the linear order of the PFs, in contrast with the orderly stretch observed in [85].

To distinguish formally the orderly shift of PFs from shuffling in more general environ-
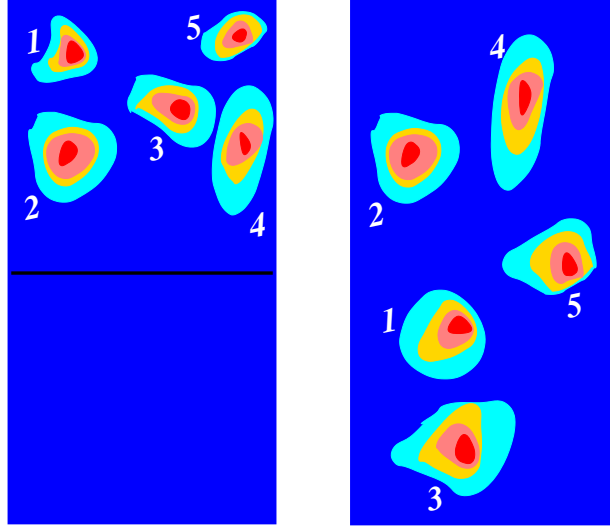
FIG. 5: Remapping caused by the global abrupt change of the environment (Mumby box). The order of the 5 PFs in the upper half arena changes completely after the barrier (black line) is removed.

ments, a PF configuration can be associated with an auxiliary graph G, defined e.g. as the Delaunay graph of the Voronoi tesselations of the PF layout [57, 144, 185].

For a given PC/PF, its Voronoi region is defined as the set of points on the arena that are at least as close to the point of its maximal firing rate as to the maximal rate point of any other PC. The Voronoi region of a given PC has no a priori geometric relationship to its PF – e.g. it may contain its PF or be contained in it. Once the Voronoi diagram for a given PF layout is obtained, its dual object, the Delaunay graph, G, is built by connecting the maximal firing rate locations of neighboring Voronoi regions by an edge. With these objects at hand, the regime of regular responses to the slow changes can be defined when the graph G is "continuously deformed", i.e. although the Voronoi regions change, the connectivity of G does not, whereas remapping corresponds to the case when the *topology* (connectivity) of the graph G is altered, i.e. the remapping can be defined as a transition between two equivalence classes of the corresponding Delaunay graphs.

This definition not only allows different partial descriptions of the PFs structures that are due to the same state of the network to be related to each other, but also to relate PF partitions that are generated in different, but "close" states of the network.

It is also clear that the correctly defined order should reflect the actual structure of

the space rather than the structure of a given set of PFs that happened to be detected in a particular electrode configuration. This implies for example that if additional PFs are detected (e.g. by adding an extra electrode), the original graph G should be considered as an approximation to the extended graph G', that is obtained by an appropriate insertion of vertexes (new PFs) and edges [15, 57]. Hence the *spatial order* of PFs is defined as set of Delaunay graphs defined up to a continuous deformation and ordered by inclusion (graph extension).

This definition allows to relate not only different partial descriptions of the PFs structures that are due to the same state of the network, but also to associate some PF partitions that are generated in different states of the network. It is clear for example that due to a finite size range of the PFs in the experiment [84], the ordered chain of PFs, e.g. PF_1, PF_2, ..., PF_N cannot keep up stretching indefinitely with the space expansion. One would expect that at some point new PFs must appear in order to cover the additional space. In another case, if some part of the $1D$ track is inflated, then at some point the original linear order of PFs will be substituted by a more complex $2D$ order. In the case of the environment shown in Figure 1, if another rounded area is gradually added somewhere in the middle, then one would expect that the original PF pattern within the growing section will initially inflate, but then (e.g. when the size of the added space will be comparable to the size of a typical PF), some new PFs will have to fill in the new place. This may happen with or without the overall order violation. If the global order on the originally available part of the track is preserved, this geometrical deformation in the middle will increase the number of PFs and turn the linear order of the PFs on the straight section into a $2D$ order from the same equivalence class. Similarly, some PCs may shut off if their PFs are squeezed out of a contracting track, which also does not violate the spatial order. In either case, if the original pattern is only amended, not scrambled, by the new fields, the original topological order is preserved. According to the above definition such restructuring will not qualify as a remapping.

It should be emphasized that this definition of the PF order via graph topology helps only to separate the regime of continuous changes from the remapping events, however it does not necessarily specify either the state of the network or mark the topology of the inner space. The graphs from different equivalence classes may represent an inner space of same topology, and the PF partitions generated by different states of the network can be

described by equivalent graphs. The problem of defining the topology of the inner space can be addressed through analysis of the connections between the PFs, which would require an entirely different analysis, outlined in the Section VIII.

VII.   PF COHERENCE

The properties of the PFs indicate that an external observer can build a qualitative *quasi*-topological description of the space that reflects the internal structure of the space perceived by the animal.

However, the statement that the rat itself possesses an explicit map of space implies more than a mere availability of the information the locations or than completeness of this information for an external observer. Having a set of space tags does not necessarily imply having an internal space, in the same way as having a database of postal addresses does not amount to having a spatial map that facilitates or even permits navigation and orientation. The complete space information provides a vast framework that allows a countless variety of nontrivial navigational tasks to be addressed, as well as the building of spatial consistency schemes,spatial planning, etc.

The information contained in separate PFs may not necessarily be organized to produce an "inner space" [122, 162]. An alternative to possessing an emergent internal inner space produced by a specially coherent organization of the network computations might be a certain organized database of ordered links, connections, that are not necessarily geometrized or geometrizable (analyzing the database of links between French internet websites will not lead to reconstructing the geographic map of France). The emergence of an inner space would imply that the system actually knows how to associate the PF regions together on a global scale to produce a self consistent, globally coherent, explicit spatial map. The main argument in support of quasitopological inner space in the hippocampus comes from studying the coherence of the PF collective responses to external changes, which show that the behavior of the ensemble of the PFs can be better understood on the level of the properties of the inner space as a whole, rather than an assembly of individual links between location tags. Hence the nature and the mechanism of connectivity between PCs is of great importance.

Previously mentioned facts about the collective and coherent responses of the PFs to the changes of the environment, either in a local spatial frame or especially in global shifts
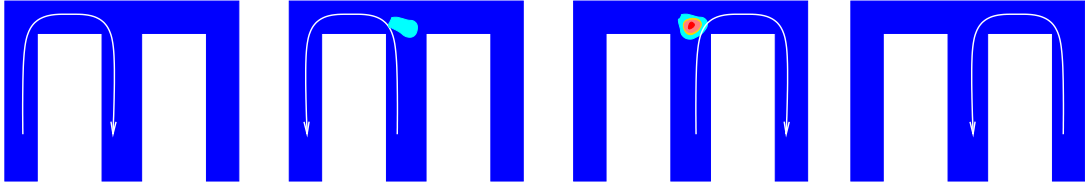
FIG. 6: A schematic representation of the activity of a CA1 place cell showing prospective coding on a W track [74].

or moves of the PFs as in [85] as well as global remappings in response to relatively local changes, strongly suggest that PC activity should always be considered in the context of the global state of the network and collective behavior of the PFs. Interesting evidence is provided by the observation of replays of the correct (direct or reversed) sequences of PCs in wake [72] and asleep [120, 178, 203] animals, which reflect the pattern of the same cells during actual spatial navigation. This result shows that correct PF sequences can be pinged by the system which remains in a state mapping state during animal's sleep.

An important support for functional connectivity between PCs comes from the phenomenon of prospective coding, found in [75]. In this experiment a rat was running on the "W-track" alternating the left and the right turns on its outbound journeys from the middle to the side arms. Interestingly, a cell with the PF located at the spot where the left and the right trajectories split, was active only if the rat was going to turn to the right, and the same cell would be silent at the same spot, if the rat's intention was to turn to the left. Such behavior indicates that PCs are not just "place" cells, but rather cells that code for a place in a particular spatial and sequential context, so some larger scale connections are involved in these cells' activity [13, 70, 131, 142].

Since deformations of the linear tracks do not cause remapping of the PFs, it is likely that the cells exhibiting prospective firing in the arena of particular geometrical configurations (e.g. W-track) will retain their functional properties if the environment is gradually deformed. From the point of view of the SRE observer such prospective firing does not provide any additional information about the geometry of the environment. Instead, it may indicate the existence of a functional connectivity between the PCs and unite continuously the PF pattern into a single space coding ensemble both in static configuration and through

the gradual geometrical changes of the environment.

An additional mechanism for local and global synchronization of the PC activity is provided by the global EEG potential oscillations, such as the θ rhythm. A number of studies have indicated that the *theta* rhythm helps organize sequential encoding and read off hippocampal information [91, 92, 118, 119]. The overall evidence suggests that one should regard the fact that a cell is active in a certain region not just as mere "place markings", but rather as "marking the location within a particular structured pattern of other locations".

At the cognitive level, structural coherence of the hippocampal memories is manifested in the phenomenon of episodic memory, i.e. the ability to put a specific memory into the context of preceding and succeeding events, as well as the ability to produce complete memory sequences from a single structured input [63]. It is well known that in humans damaged or lesioned hippocampus leads to severe impairment of these capacities, which implies that the hippocampus naturally embeds memory elements (e.g. memories of spatial locations) into a globally structured context. The pattern of difficulties faced by the animals with hippocampal damage in solving various cognitive tasks in changing environments shows that the activity of the hippocampal network is also essential for the ability to recognize persistent patterns. Even if the overall cognitive structure of the task and the general relational (topological) structure between salient features of the changing environment remains the same, animals (e.g. rats and humans) loose the effective ability to navigate among familiar cue patterns and to put separate cues and memories into the previously familiar general context.

The existence of a global map is also indicated by the phenomenon of the so-called "path integration" [65], i.e. the ability of the animals to find a direct path back to the origin of their journey after traveling along geometrically complex trajectories. However, path integration does not appear to be a hippocampal function [4], as the ability of path integration is not impaired in animals with hippocampal damage, and reflects a more general cognitive brain functioning [161].

VIII.   TOPOLOGICAL ANALYSIS OF SPACE CODING

The above discussion of the nature of the PC space coding allows the space reconstruction task in the SRE experiment to be specified by reducing it to the task of extracting the quasitopological spatial frame encoded in the spiking data.

Conceptually, the task of reconstructing the space *as perceived by the rat* is different from the task of reconstructing the space that the SRE observer expects to see. In the latter case the observer verifies the consistency of the received rat's PC signals with his own representation of the environment, and in the former case the goal is to establish the internal consistency of spatial relationships assuming a specific space coding mechanism. The hippocampal topological basis of the perceived space can be understood as the state of the hippocampal network, that is directly experienced by the animal and that is projected onto the observed environment via PC activity as a partition of PFs. To emphasize this distinction between the observed and "inner" spaces, the first task will be referred to below as the *inner* space reconstruction experiment (ISRE).

In either case, the underlying assumption is that the firing fields are associated with the neighborhoods U_i of a topological space X and hence the PC information must be consistent with possible spatial relationships between the neighborhoods of X. In the SRE context the topological space in question is the environment S as verified directly by the observer, and in the ISRE case it is the topological skeleton of the hypothetical "inner space" $\tilde{S}$ in which the animal perceives itself, so the ISRE observer in effect induces the structure of the "inner PFs" covering the inner space of the animal from the activity of PCs.

In both cases the analysis of the encoded space is based on the fact that the topological properties of a space can be deduced from the properties of its coverings by open sets U_i (neighborhoods) defined either directly or via some additional structures, associated consistently with the neighborhoods. Such analysis allows the topology of the space to be characterized in terms of topological invariants [146]. In the case studied here, the structures associated with neighborhoods are the firing rates of cell populations, which can be used to identify the topology of the environment both in the SRE and in the ISRE contexts for different PF layouts, and to argue that the topology observed by the experimenter is equivalent to the topology of the rat's own inner space.

Mathematically, the task of establishing a global arrangement of locally defined structures

FIG. 7: Intersection of two regions x and y, inclusion of regions and separated regions.

over a topological space X is a well defined problem that in its most general form is addressed in the so-called sheaf theory [81, 94, 121, 181, 186]. The concept of a sheaf captures the idea of associating the local information with the spatial structure of a topological space as a whole [206], and can provide a general framework for analyzing different types of neural information associated with the topological structure of the environment, such as the angular orientation at different locations (spiking rates of head direction cells) [173, 183, 184] or the state of running straight or turning (cells in the parietal cortex) [31, 145]. So from the perspective of the topology reconstructing task, the (I)SRE goal is to define the structure of the topological space based on the PC firing information, i.e. to associate the local PC information into a global topological characteristics of the "inner space" as a whole.

In the context of studying a rat's mechanisms of space coding, the PFs appear to be primitive regions, in terms of which more complex spatial objects are constructed, both smaller or larger than a single PF. Although it may be possible that for the rat itself, spatial awareness is based on the analysis of currently coactive PCs, the analysis made by the (I)SRE observer can include any relationships between PCs/PFs that were observed in the course of a (I)SRE experiment.

Let us assume that for a given set of k cells and the corresponding threshold levels θ_i, $i = 1, ..., k$, the PF data is sufficiently complete, so that the PFs produce a complete covering of the environment,

$$\cup_i PF_i^{(\theta_i)} = E. \tag{1}$$

The regions can be defined as the rat's position states in which the firing frequencies, $f_1(t)$, ..., $f_k(t)$, of a selected set of PCs, $c_1, ..., c_k$ vary within chosen limits, $f_i \in \Theta_i \equiv \left[\theta_i^{\min}, \theta_i^{\max}\right]$. The union, the inclusion and the intersection of the regions (Fig.7) can be defined immediately via the corresponding union, inclusion and intersection of the firing rate intervals Θ_i of two cell populations. For example, x is a subregion of y, $x \subseteq y$, if whenever every place cell

defining x is firing at greater rate than its threshold, then so is every cell defining y.

Since for example a region $V = PF_1 \cap PF_2$ is contained in $U = PF_1$, the restriction operator i_{UV} from U to V corresponds to selecting the rat position states in which both cells simultaneously have a high firing rate. Clearly, for the three nested neighborhoods $W \subset V \subset U$, the restriction from U to V and then to W (region of coactivity of 3 PCs) and the direct restriction from U to W, will yield the same result, i.e. $i_{V,W} \circ i_{UV} = i_{U,W}$. It is important that such analysis of the "covering" can be made directly in terms of the firing properties of the PCs that does not refer to the externally observed geometrical PF features, and does not require observing the behavior of the rat or knowing its environment. It is also important that the restriction operation does not depend on the restriction sequence. As a result, the firing rate of the whole PC population can be extended in a unique way to form a continuous function $f : U \to R$ which agrees with all the given f_i. This provides the topological characterization of the space in terms of well defined topological invariants, based on the analysis of its coverings.

With a given set of the regions U_1, ..., U_n, covering the environment, one can associate the following multidimensional polytope (simplex) also called the "nerve" N of the covering [207]: 1) The vertexes $\sigma_i^{(0)}$ of the simplex correspond to the individual regions U_i. 2) The edges $\sigma_{i_1 i_2}^{(1)}$ correspond to overlapping regions, $U_{i_1} \cap U_{i_2} \neq \emptyset$, i.e. to the coactive cell populations. 3) The two dimensional simplexes (facets) $\sigma_{i_1 i_2 i_3}^{(2)}$ correspond to triple intersections $U_{i_1} \cap U_{i_2} \cap U_{i_3} \neq \emptyset$. 4) In general, k–simplexes $\sigma_{i_1 i_2 \ldots i_{k+1}}^{(k)}$ correspond to nonempty intersections $U_{i_1} \cap U_{i_2} \cap \ldots \cap U_{i_{k+1}} \neq \emptyset$, or a set of $k + 1$ coactive PC sets.

In particular, one can consider coverings generated by the PFs themselves and the corresponding simplex generated by the peaks of activity of PCs, the overlapping PFs, $PF_{c_1} \cap PF_{c_2} \neq \emptyset$, the coactive triples of PCs $PF_{c_1} \cap PF_{c_2} \cap PF_{c_3} \neq \emptyset$, etc. The analysis of the (I)SRE observer is based on studying the topological structure of the resulting simplicial complex using an appropriate system of algebraic indexing of the simplexes. The topological properties of the space can be revealed via the structure of the space of linear functions on the simplexes, $\alpha^k(\sigma_{i_1 \ldots i_{k+1}}^k)$ – the cochains taking values in properly selected set of coefficients F, e.g. 0 and 1. The region restriction operation i_{UV} allows the functions defined on k-simplexes to be put "into the context" of the higher dimensional $(k + 1)$-simplex that they enclose, via the so-called "codifferential" operator δ [94, 146, 181]. The resulting algebraic structure defines the set of topological invariants that uniquely characterize the topology of
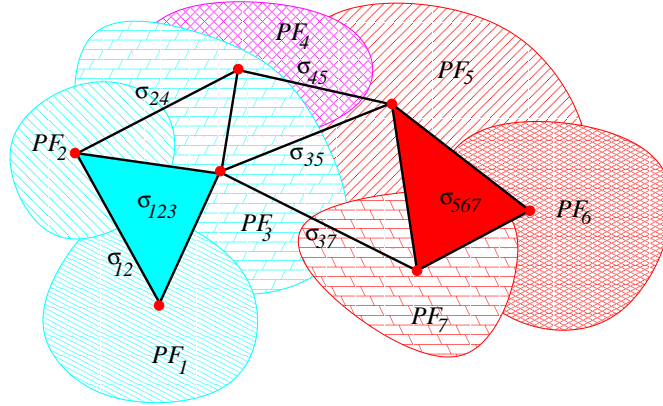
FIG. 8: Simplex generated by a covering of a plane environment.

the simplex – the Čech cohomologies of the covering, $H^q\left(N\left\{U_i\right\}\right)$.

If additional PFs are observed in (I)SRE, the old nerve of the covering will be inscribed into the new one, $\varphi_{UV} : N\left\{U_q\right\} \to N\left\{V_p\right\}$, so the refinement of the simplex induces a mapping of the topological indexes

$$\varphi_{UV}^* : H^q\left(N\left\{U_i\right\}, F\right) \to H^q\left(N\left\{V_i\right\}, F\right). \tag{2}$$

Such analysis allows the topology of the environment to be characterized using nonequivalent (in the sense of the Section VI) coverings that are generated during the remappings. If both new and old coverings are defined via singly connected, contractible in the topology of X PFs, they define the nerve of the simplex of the same cohomological type, so different PF coverings of the same environment must provide equivalent topological representations of it. This also shows that unlike the topological order of the directly observed PF partition (i.e. the topological class of the Delaunay graph) the topology of the inner space is not violated in remappings.

Furthermore, a basic (but important) result from the algebraic topology states that in case if X is a manifold and if the covering is such that all $U_{i_1} \cap ... \cap U_{i_{k+1}}$'s are contractible, e.g. small convex regions in the metric of X, then the nerve of the covering is homologically equivalent to X,

$$H^*\left(N\left\{U_i\right\}\right) = H^*(X), \tag{3}$$

so the topological (cohomological) characteristics of the covering are identical to the topo-

logical characteristics of the manifold itself. This simple result allows the (I)SRE observer to make judgments about the topological properties of the environment as a whole and in particular to conclude that the topology of rat's "inner space" coincides with the topology of the environment defined via explicitly observed PF coverings. This equivalence also shows that the hippocampal space representations of different rats can be mapped one onto another.

It is interesting to mention that the results and the methods obtained above might be used for extracting the global spatial topological characteristics of PC activity patterns not only from awake animals, but also from the PC replay data collected during animal's sleep [105].

Certainly, the possibility to compute correct topological invariants depends crucially on the quality of the covering, i.e. on the availability of a sufficient number of the PFs. Usually the environments in which the behavior of a rat is studied have geometrically simple form, so it is assumed for simplicity that the environment is covered by a sufficient number of PFs. In case if the geometry of the environment is complex, the derivation of the correct cohomological characteristics becomes a more subtle problem [14, 39, 51, 52, 82, 124, 166, 167, 205], that can be helped by the local analysis of the spatial relationships encoded by the PFs.

IX.   QUALITATIVE SPACE REPRESENTATION. RCC

The mathematical formalism used above for describing the *global* topological properties of the space does not however provide a framework for a practical, biologically plausible analysis of the current, local PC firing configurations. It does not necessarily suggest a scheme for a *local* spatial information processing that can serve as the basis of the local spatial planning, navigation and in general for *spatial reasoning*. On the other hand, there exists a variety of qualitative space representation (QSR) methods [43], which provide practically useful and conceptually complete approximate representations of space that include local topological information analysis. The reasoning techniques within different QSRs provide case specific formal languages and logical systems that include the notion of spatial proximity and other necessary spatial relationships. These languages can provide a complete description of arbitrarily complex spatial reasoning schemes used for navigating, spatial planning and

establishing spatial (in)consistencies, which have been studied in a number of mathematical [42, 43, 160] as well as applied contexts, such as organizing geographical databases, robotics, artificial intelligence, object recognition, etc. (e.g. [62, 66, 71]) and including some bio-applications [53, 68] but not to our knowledge, the task under consideration here.

A simple example of qualitative spatial reasoning is provided by the above analysis of a linear sequence of PFs on a linear track, that allows the SRE observer to conclude that the space the rat has explored is linear and how many ends it has. If the cell population activity patterns are always consistent with a simple linear (direct or reversed) sequence a_1, a_2, ..., a_n, then the SRE observer can conclude that the track is linear. The violations of the linear order via $a_1 \rightarrow a_n$ or $a_n \rightarrow a_1$ transitions only, signify that the track is circular, while presence of "forking" sequences signals branching arms of the track, etc. (assuming no inconsistencies would be expected in actual biological recordings in stable hippocampal state).

A more general form 1D reasoning is addressed by the so-called Allen Interval Calculus relations reasoning calculus [3]. The trajectory reconstruction mentioned in the Section II also in effect represents a simple example of qualitative spatial analysis.

In general, QSR methods can be applied to representations derived from analogical representations based on explicit maps or on database representations of spatial relationships (e.g. statements like "the book is in the bedroom on the table that is to the left of the window"), as well as on a combination of both. The advantage of the explicit map is that it can provide (typically at a higher computational cost) a basis for generating task specific spatial relations, while in the second (reactive) case the relationships are not defined at all unless stated explicitly (e.g. if no relationship is specified about where the table or the book are in relation to the chair, there is no way to deduce that – unless it can be inferred indirectly via the relationships to one or more other objects). Different QSR schemes could be used to represent different aspects of space coding in various brain parts [31]. In the cognitive space coding schemes, QSR methods may be used for describing the relationships between behaviorally relevant or otherwise salient spatial locations [49, 55], i.e. in establishing the cognitive "spatial salience map" of the environment. On the other hand, the hippocampus seems to possess an explicit spatial map that produces the topological skeleton of the inner space.

A practically convenient QSR method for describing topological spaces is provided by

a pointfree method called the Region Connection Calculus (RCC) [42, 43, 88, 160], that can be used for studying the quasitopological space that emerges due the hippocampal PC activity. In its general form, the RCC method unifies several QSR schemes that are based on a single primitive, binary, reflexive and symmetric connectivity relation $\mathsf{C}(x, y)$ (region x connects with region y), that relate every two regions of space. In the context of the (I)SRE analysis, $\mathsf{C}(x, y)$ can be evaluated directly as the coactivity of the cell populations above the corresponding threshold levels, hence the RCC analysis can be used directly in the space reconstruction setup.

From the point of view of the (I)SRE analysis, it is important that (see e.g. [42, 43, 88, 160] and the references therein) that the RCC relationships form predicates of a *first-order logical system*, which turns the spatial reasoning based on the PF information into a logical calculus, a formal mathematical theory, in which reasoning can be done based on formal logical symbol manipulation.

The resulting logical language can be applied to in depth, intrinsic analysis of the PF information. To begin with, such an analysis could be used to decide whether the relationships encoded in the firing patterns actually permit the "spatial order" interpretation. Specifically, the consistency of the *hypothesis* that the firing patterns of a certain collection of neurons (e.g. hippocampal or visual cortex cells) encode spatial relationships, in which cofiring of two cells represents the overlapping of the corresponding regions, can be conclusively tested using the RCC analysis in finite time, that grows polynomially with the number of the given "cofiring" relationships. Such an approach provides an interesting example of a mathematical (logical) identification of the computational nature of the receptive fields.

There exists a number of phenomenological models that aim to explain the observed properties of the PF regions based on common qualitative relations between PFs and the geometrical features of the environment (the "geometric determinants") [30, 32, 90, 150, 190]. These approaches exploit the experimentally observed trends in rat's spatial behavior and its "spatial instincts", such as marking the behaviorally important areas (e.g. dead ends of tracks, food reward locations, etc.) as "places", and use some phenomenological knowledge about the global behavior of the PFs [67, 85, 139, 140, 141]. However, mere description of such PF's associations with corners and walls in itself does not provide a key for understanding the scope and the nature of the information contained in the hippocampal computations, as well as the reasoning structure based on it. However, the RCC topological calculus the
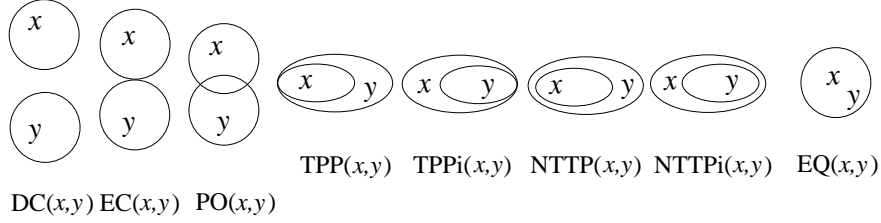
FIG. 9: RCC8 relationships.

analysis further to be taken further: given a certain initial amount of information, such as e.g., the association of several PFs with some "geometric determinants", the (I)SRE observer can reason logically about the sequence of PC activations in order to understand an animal's navigational strategies at the topological level, based on logical (arithmetical, mechanical) symbol manipulation, defined by the RCC logical calculus.

Within each particular RCC formalism, spatial order is defined via a family of binary topological relations imposed on the regions, that guarantee the consistency of the space constructed from them. The most widely used formulation of RCC[42, 43, 88, 160] defines 8 jointly exhaustive and pairwise disjoint (JEPD) binary topological relations between pairs of regions with $c$risp boundaries; this calculus is known as RCC8 and can be defined from the single primitive $\mathsf{C}(x,y)$ in a full first order theory, or the relations are taken to be primitive in a constraint language setting. These relations shown in Fig.9 are: DC (x is disconnected from y), EC (x is externally connected with y), PO (x partially overlaps with y), TPP (x is a tangential proper part of y), NTPP (x is a nontangential proper part of y), TPPi (inverse of TPP), NTPPi (inverse of NTPP) and EQ. Axioms can be introduced to define regions corresponding to the complement of a region, the sum, the difference and the product of a pair of regions – in the cases when they can *logically* exist.

Interestingly, these RCC relationships are also manifested at a cognitive level [109, 163]. In each PF layout, every pair of PFs can be related to one another via one of the JEPD relationships from a chosen RCC calculus, based on the analysis of the PC firing rates. The regions inferred via RCC Boolean functions may or may not be realized as actual PFs, however *logically* they are available for spatial reasoning both to the (I)SRE observer and to the animal, and hence they help the observer to follow spatial aspects of the animal's behavior
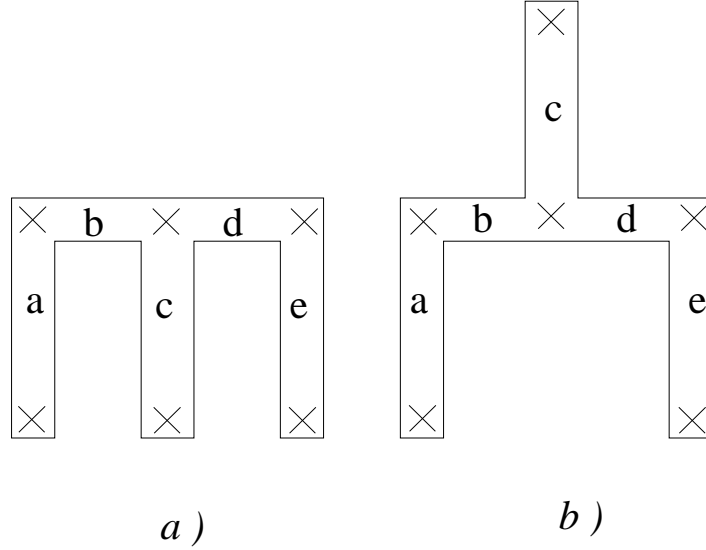
FIG. 10: W track, with 5 basic connected component parts and 6 marked points (geometric determinants).

and its navigational strategies. Hence RCC provides a practical tool for reconstructing the specific relationships between the regions coded in the hippocampal network and a clear logical scheme for spatial reasoning. For example, the RCC8 based analysis can be applied to describing the spatial structure of the "W" linear track. As mentioned in Section IV, one of the biologically relevant distinguishing features of linear tracks is that some pairs of parts can be shrunk to a point whereas others cannot. For the 5 connected basic regions of the W track shown on Fig.10 a) that cannot be divided into two disconnected (DC) parts, the pairs (a, b) or (b, d) are contractible but (a, c) or (b, e) are not. The RCC8 relationships between the regions that describe the structure of the W track environment are $\mathsf{EC}(a,b)$, $\mathsf{EC}(b,c)$, $\mathsf{EC}(b,d)$, $\mathsf{EC}(c,d)$, $\mathsf{EC}(d,e)$, $\mathsf{DC}(a,c)$, $\mathsf{DC}(a,d)$, $\mathsf{DC}(a,e)$, $\mathsf{DC}(b,e)$, $\mathsf{DC}(c,e)$. Hence, the (I)SRE observer will immediately be able to infer the W (Fig. 10 a) or topologically similar (Fig. 10 b) structure of the track using RCC5 calculus, if the relationships between different pairs of (connected) PFs regions detected in the experiment (notably $\mathsf{PO}(PF_i,PF_j)$ and $\mathsf{DR}(PF_i,PF_j)$) are compatible with these relationships. Given a sufficient number of PFs, it is also possible to determine the structure of the environment in cases when the regions are multiply connected, however this case involves a more complicated analysis.

It is also conceptually important, that in the case of the PF, the regions "emerge" from
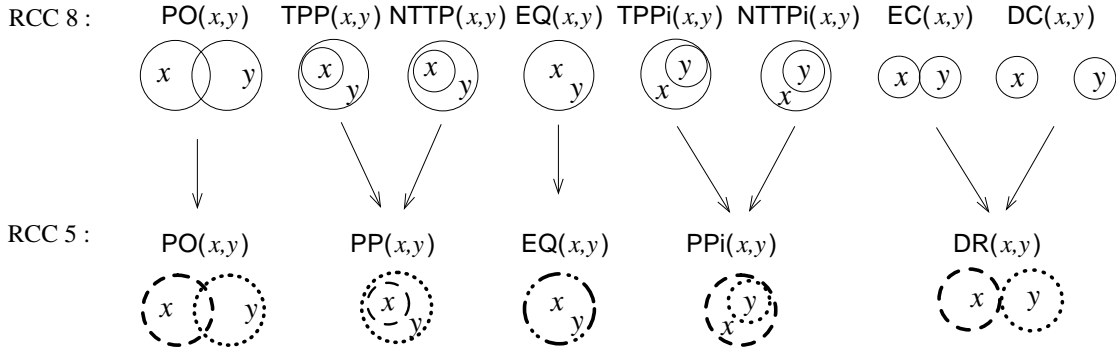
FIG. 11: RCC8 goes into RCC5. Dashed and dotted lines represent region boundaries in RCC5 approach.

the discrete spiking patterns. Since at any moment of time t and for any chosen frequency thresholds θ_i there exists only a finite number of spikes that define a region, the regions and their boundaries are "soft", in the sense that the tangency relationships, such as (TPP versus NTPP), generally cannot be distinguished. As the statistical information about the PC firing accumulates with time, the regions associated with PFs become sharper in static environments both to the observer and to the rat. This argument suggests the of use of the RCC5 calculus, which is the result of ignoring tangency relationships in RCC8 and thus has a smaller set of JEPD relations to describe the relationship between two regions: DR (discrete), EQ (identical), PP (proper part), PPi (inverse PP), and PO (partial overlap), could be used instead – see figure 11. Different choices of the threshold will generate a stack of the soft boundary regions that are related to one another via one of the RCC5 relationships.

It is important that the JEPD relationships between naturally "fuzzy" PF regions are also vague, in the sense that they emerge together with the PF themselves, as the number of spikes fired in a specific configuration accumulate. However, since the data accumulation happens gradually, the logical study of the emergence (of "crisping", [44]) of the regions *and* of the relationships between them can be made based on the analysis of the possible gradual transitions between the relationships. As shown in [42, 43, 160], the RCC relationships can be organized into natural succession sequences (conceptual neighborhoods) that specify the logical order in which RCC relationships between the regions can change. This provides a
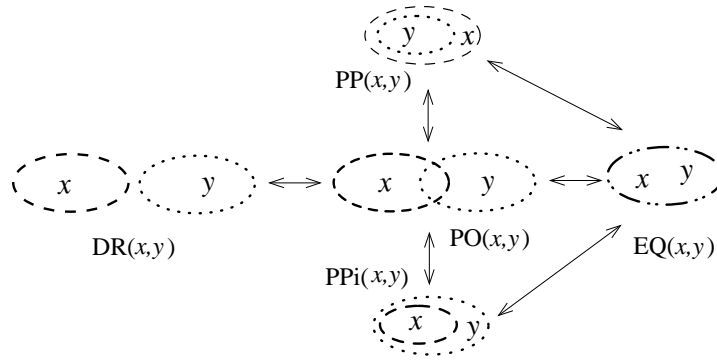
FIG. 12: The immediate conceptual neighborhood structure of RCC5 – the possible sequences of gradual transformation of the binary JEPD relationships.

possibility to follow the intriguing process of the emergence of the region-defined space.

Remarkably, RCC conceptual neighborhood analysis has the potential not only to follow the development of the spatial relationships in static environments, but also to follow the changes in the PF configurations in the regime of smooth continuous transitions. Hence the (I)SRE observer can reason and resolve the space reconstruction task not only in static, but also in "flexible" tracks and arenas.

In addition to "natural" fuzziness of the PF regions that is due to the discreteness and stochasticity of spiking information, PFs are arbitrary defined by the randomly selected value of the firing threshold θ_i. As mentioned above, any set of n thresholds $f_{i,\alpha} \in \left[\theta_i^{\min}, \theta_i^{\max}\right]$ $\alpha = 1, ...,n$, will produce a stack of n soft boundary regions related to one another in RCC5 calculus via PP or PPi relationships. This "stack of regions" (even in the simplest case $n = 2$) actually creates additional possibilities for the analysis within the so called "egg-yolk theory" [44, 46, 47, 114] and its generalizations, which describes vague regions using a formal "nested" structure – an inner "yolk" representing space that is definitely part of the region (for the yolk the threshold can be set sufficiently high) and the "white" between the yolk and the rest of the environment, representing space that may or may not be part of the PF. The threshold for the white (not-PFs) boundary can be set rather low to admit space that is not a part of the PF. Different egg-yolk versions of RCC5 with varying numbers of JEPD relationships [44] can be used for a specific logical analysis of a given PC data set.

X.   DISCUSSION

The analysis of the spatial tuning of the hippocampal PCs and the behavioral manifestations of the hippocampal memory structure suggests that the representation of the information in the hippocampal system is based on explicit quasi-topological maps. Overall, the existing experimental evidence seems to indicate that the hippocampus encodes order relationships, which, in spatial context, translates directly into the topological order of the space in which the rat navigates. Although the PFs are tied to various geometrical features in the environment, e.g. corners, walls, objects on the arena, etc. [149], the spatial information stored in the hippocampal network appears to be of a predominantly topological nature.

The hippocampus is believed to perform indirect associations between various memory and sensory patterns [129, 137], which leads to the appearance of a structural representation of the environment. In particular, it appears that the animal internalizes a flexible discretized representation of space by "memorizing" an allocentric plastic grid of place fields. According to the view proposed above, the pointfree topology framework allows hippocampal activity in a stable regime to be interpreted as a manifestation of an emergent quasitopological inner space, whereas the RCC calculus allows the use of the information provided by the PCs to reason about its internal organization. The power of the RCC method is that it provides a nontrivial logical spatial reasoning scheme based on only a small number of PFs recorded in the experiment, which makes it specially valuable for the real data analysis.

These principles of the spatial information representation and processing reflect the general structure of memory organization. From the biological point of view, the existence of a topological reference map stored in the brain enables the animal to track the "small changes" of the sensory input by putting them into a continuously defined context, as opposed to having to evaluate anew every sensory configuration without recognizing patterns of continuous change. Biologically, this may be related to the fact that an animal's survival depends on its ability to single out salient changes in the environment as reliably and at the same time as flexibly as possible. The animal must be ready to change its perception of the environment on the time scale at which the external "threats" may occur. Often it is impossible for the animal to know when and how its navigational task may change, hence its behavioral decisions must be made based on spatial encodings which do not precisely

determine spatial location mechanisms [20, 21, 44, 93]. It is nevertheless clear that having a perfectly correct but vague solution to a fuzzily posed task is certainly biologically more effective than spending time on producing computationally costly and certainly inaccurate precise answer.

Generally, in order to understand the neural mechanism of space perception, one needs to understand how the representation is created, learned, adjusted, etc., as well as its functioning principles, i.e. how the resulting map is used. The first question is addressed by various dynamical or statistical network models that aim to reproduce, based on physiological data, the overall functioning properties of the hippocampal network and its interaction with the other brain parts [104, 172, 193].

Our analysis of the second question suggests a topological interpretation of the hippocampal spatial maps and their further understanding in the framework of the pointless topology and the QSR (RCC) spatial analysis and reasoning methods.

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XI.   APPENDIX. PHYSIOLOGICAL PROPERTIES OF THE PLACE CELLS

Let us briefly outline some general physiological information concerning the PCs and properties of PFs based on the rat data. Physiologically, the hippocampal formation has several parts (CA1, CA3, Dentate Gyrus, and Subiculum) which are subnetworks of different architecture and functionality [6, 96, 195]. Cells in all of these parts have PC properties, however their spatial tuning (PF sizes, quality, responsiveness to external changes and so on) are different. Below we will discuss the PFs and PCs based mainly on the properties of the CA1 cells, which are the most commonly studied PCs of the hippocampus.

1.   As a result of exploratory learning of the environment, the hippocampal network falls (through some rapid plasticity mechanism [22]) into a particular *global state* $S^{(i)}$, characterized by a particular set of intercellular connections strengths, which yield a specific kind of activity pattern [141]. In case of a linear track, PFs appear after 4-5 mins (a few runs across a few meter long track) and in open arenas of similar size PF form in 10-25 minutes and take a few days to stabilize. The settling of

the network into a particular state is often described by various attractor network [171, 192, 193] or statistical (spin glass) models [77, 191] in which each state $S^{(i)}$, $i = 1, ...,$ is represented by a local (in parameter space) dynamical regime or local minima of appropriate statistical weight functionals. In either case, the existence of (dynamical or statistical) basin of attractions references the fact that as long as the outside world provides a steady flow of incoming sensory stimuli that does not imply any significant changes of the environment for the rat, the hippocampus as a whole remains in the same regime in which every cell "knows its place" with respect to other cells in the network, and the sensory input simply triggers the firing events. The size of the basin of attraction (depth of the local minimum) and the stability of $S^{(i)}$ depend on many factors, e.g. on how long the animal was learning the environment, in what sequence [202], etc.

2.   It is clear that different parts of the environment can be distinguished from each other because each location is characterized by its own combination of physical (or idiothetic) cues, which produce a particular set of sensory inputs that the rat receives at (or in the course of getting to) that location. However, it is important that the rat can map the same environment in many different ways [79, 182], so the same combination of sensory inputs may produce entirely different patterns of hippocampal activity in the same rat, depending on the state of its hippocampal network. Moreover, the PCs can retain their firing regime even if only a partial sensory input (compared to e.g. the sensory input when the environment was being learned by the animal) is present. For example, the animal can retain its system of PFs if the lights are dimmed or even in complete darkness [126]. Hence, although in wake animals it is primarily the sensory input that triggers the PC activity, however it is not just a simple "funneling" of the sensory input into the hippocampus that is responsible for the firing of the PCs. PCs can also fire in the right navigational sequences during spontaneous network activations while the animal is asleep [72, 120, 178, 203]. To emphasize this point, below the state $S^{(i)}$ will be referring to the overall *regime* in which the network operates, its global configuration, as opposed to the current spiking activity level of the hippocampal cells. Certainly, the state of the network can also change, but this change happens on a different time scale during a catastrophic restructuring (remapping) event.

3. The structure of $S^{(i)}$ imposes a particular discretization scheme onto the sensory input and a particular sequence of the firing activity shift from cell to cell. Hence the activity of the hippocampal network in the state $S^{(i)}$ produces a partition of the environment into a discrete collection of overlapping regions (PFs), so $S^{(i)}$ encodes the environment in an explicit *global*, i.e. simultaneously defined for the whole environment, map.

4. The sizes and the shapes of the PFs corresponding to different PCs can vary significantly. The same cell in different environments or in a different space mapping state $S^{(i)}$ in the same environment can produce PFs of completely different sizes and shapes. Typically linear sizes of PFs range between 10 to about 75 *cm* [16]. In certain cases PFs can be as big as the size of the whole environment accessible to the animal – e.g. 10 meters in diameter. Typically PFs are compact, convex (convexity and other shape features of PFs can be modulated by the environment, e.g. by a curving of a track) regions of space. In some cases PCs can have multiply connected PFs, however one can argue that in an environment perceived by the animal as a single integral piece, each PC has a single, compact, contractible PF. No two PFs of different cells entirely coincide or even have same maxima locations, so each cell has a unique place field inside the environment. In linear environments, a PF can be directional, i.e. a PC may be active only if the rat moves in one of the two possible directions, but not in the other.

5. The peak firing frequency (about 20 Hz) of a particular cell c is reached when a rat passes through the center of its PF_c, however peak firing rates may differ from cell to cell and for a given cell from environment to environment. Outside of its PF the cell shows only some weak "background noise activity" (about 0.1 Hz). The averaged spatial firing frequency (the firing probability) of a PC as a function of the coordinates x and y produces a surface that often looks like and usually is modeled as a Gaussian hump over a compact base. As long as the rat remains in the same location, the activity level of the PC remains approximately constant [16].

6. A given point in space may be shared by many PFs. At a given location, about 300 out of $3 \cdot 10^5$ of CA3 cells and $3000 - 4000$ out of $4 \cdot 10^5$ of CA1 cells are simultaneously active, however the activity of only few of them are near maximal level [7, 96, 171].

7. One of the most important properties of the PFs is that they are *allocentric,* i.e. the spatial location of the PFs is fixed in the external world coordinate frame, regardless of the history of animal's behavior. After the animal familiarizes itself with the (static) environment and creates its PF partition, the location of each PF does not change significantly between the rat's visits. In a given state of the network, it is always the same cell that marks a given place field.

Overall, the PFs' patterns are not significantly influenced by the details of animal's behavior, the PFs layout structure can be basically "decoupled" from the animal's behavior, and hence it can be used for the analysis of the environment, rather than a combination of environmental features and the internal state of animal's brain.

8. The external location of the PF of a given cell in different maps can be very different. It is not fixed either with respect to other PFs or with respect to any particular "features" of the environment. Generally speaking, if the animal is moved from one environment E_1 into another E_2, then the PF partition of E_2 will be entirely different from that of E_1, even if both environments have similar features [177]. The old "corner" cells may mark the center of the new arena or appear in some other corner or stick along some wall segment. It seems impossible to predict from previous behavior where or even whether a cell will have its PF in the new environment before it actually appears. For a given cell in a given environment, there is about 30% chance of being active [128, 171].

9. Generally speaking, there is no commonality between the spatial position of PFs in different rats who have learned the same maze. Every rat comes up with its own mapping, i.e. its own assignment of "places" to cells (or visa versa). Overall it appears that finding a place for the PF in a given environment is a very flexible dynamical process with many parameters.

10. The pattern of the positions of PCs in the brain tissue (i.e. in the CA1 or the CA3 areas) does not correspond to the spatial pattern of the PFs in the environment. In particular, neighboring cells do not in general map to neighboring physical places. For example, the PFs of a group of nearby cells recorded from a single electrode are scattered all over the environment. In this sense, the PF mapping of the environment

to the cells of the hippocampus is not "topographical". If parts of two place fields PF_{c_1} and PF_{c_2} overlap, it does not mean that one cell can "activate" the other. If the rat enters PF_{c_1} and has not yet entered PF_{c_2}, with $PF_{c_1} \cap PF_{c_2} \neq \varnothing$, then the cell c_2 will be silent until the rat actually gets inside PF_{c_2}. As the number of the implanted electrodes and hence the recorded cells increases (currently about 150 cells can be recorded simultaneously [204]), the corresponding PFs produce progressively denser cover of the environment. The union of all PFs completely covers the environment E,

$$\cup_c PF_c = E. \tag{4}$$

However, there is a difference in PF occupancy for "interesting" places compared to "uninteresting": there are typically more PFs around food wells, maze junctions and other "important places".

11. An important ensemble characteristics of PC firing activity are the global oscillations of the intracellular potential, in particular the 8 Hz θ-oscillations [37, 38, 194], as well as the correlations between the local phase of θ-rhythm and the firing rate of a PC [153]. These oscillations play an important role in synchronization across large populations of cells, and often help to understand the functional connections between the activity patterns of different cells [91, 92, 118, 119].

Based on these properties of the PCs and on some additional observations of the PF ensemble behavior described below, the goal of the following discussion will be to provide some arguments in favor of the topological nature of the spatial representations generated by hippocampal neural activity.

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[206] According to [181], "Sheaf is effectively a system of local coefficients over a space X."

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